corresponding to the right aortic arch is present; but its presence is found in so many Accipitres that it is highly characteristic of them.

I quote from MS. of Garrod the following measurements of the various parts of the alimentary tract to show how close is the resemblance between the two:—

| | *Cariama*. | *Chunga*. |
|---|---|---|
| | in. | in. |
| Small intestine .... | 33 | 33 |
| Large intestine .... | 3 | 3·5 |
| Cæca..... | 8·75 | 10·5<br>8·5 |

The *expansor secundariorum* is as in *Chauna* and *Cariama*. There is no *biceps slip* to patagial tendon as in *Cariama*. The *anconeus* has an accessory flat tendon attaching it to humerus.

The *pectoral muscle* arises from the whole of the sternum, which is free from the origin of the second pectoral; it also arises from the aponeurosis of the second pectoral. It is partially divided by a septum into two muscles.

The *tensores patagii brevis* and *longus* appear to form one muscle at their origin; this muscle receives a tendon from deltoid ridge of humerus. The tendon of *brevis* is very large and flattened out, but as it is accurately figured by Fürbringer[1] I do not describe it more fully. A drawing of Prof. Garrod's shows that in *Cariama* the *tensor brevis tendon* is similar, and he particularly states that there is no *biceps* slip; neither Fürbringer nor myself have found a biceps slip in *Chunga*.

The *accessory femoro-caudal* is present in *Cariama*, and it is stated by Garrod in a MS. note to be missing in *Chunga*; however, I found this muscle in the specimen dissected by me; it was thin and slender, and became tendinous in the middle between its origin and insertion.

The *biceps brachii* in *Chunga* is bifid at its insertion.

## 3. On the Relations of the Fat-bodies of the Sauropsida. By Gerard W. Butler, B.A. (Communicated by Prof. G. B. Howes, F.L.S., F.Z.S.)

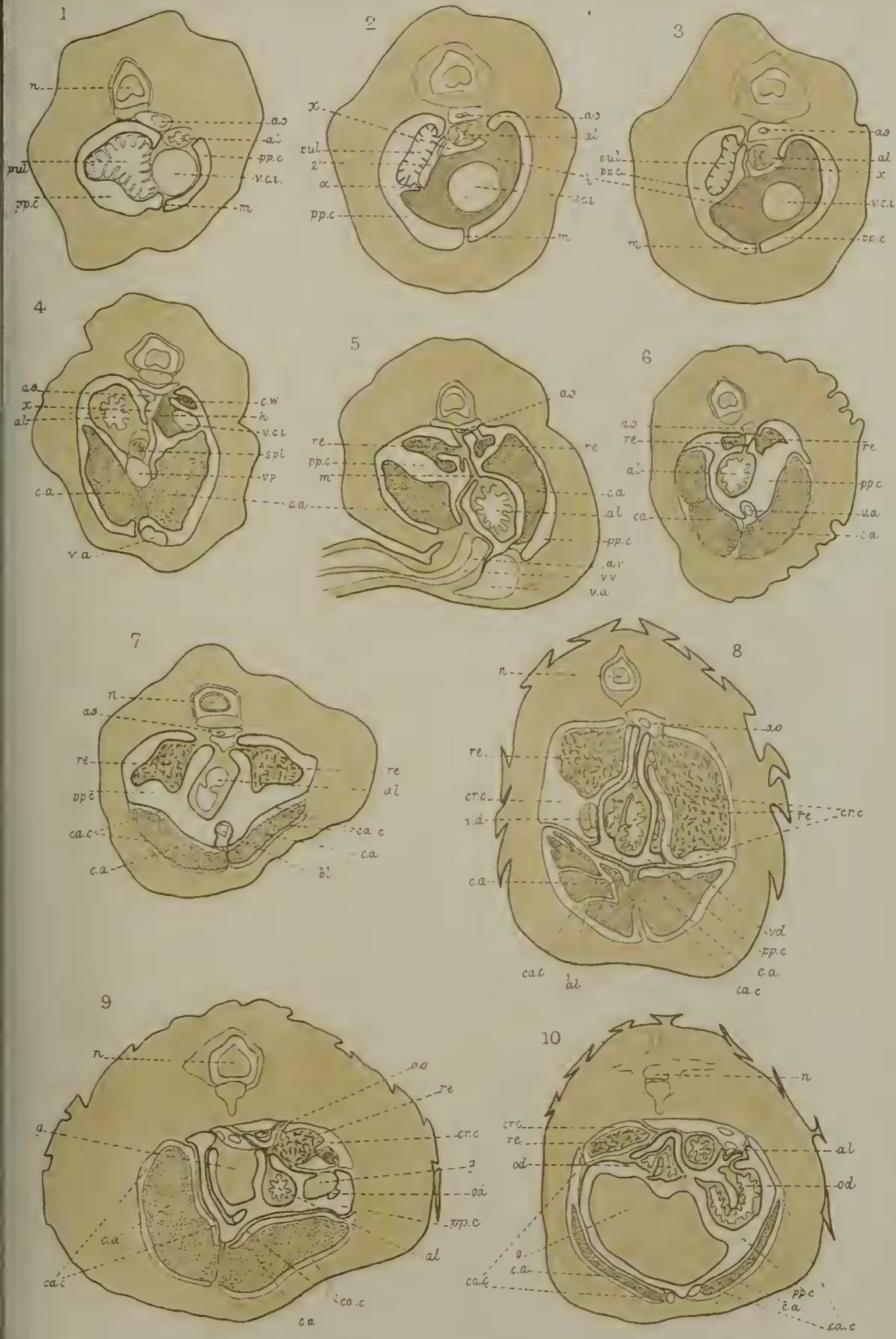
[Received November 26, 1889.]

(Plates LIX. & LX.)

Contents.



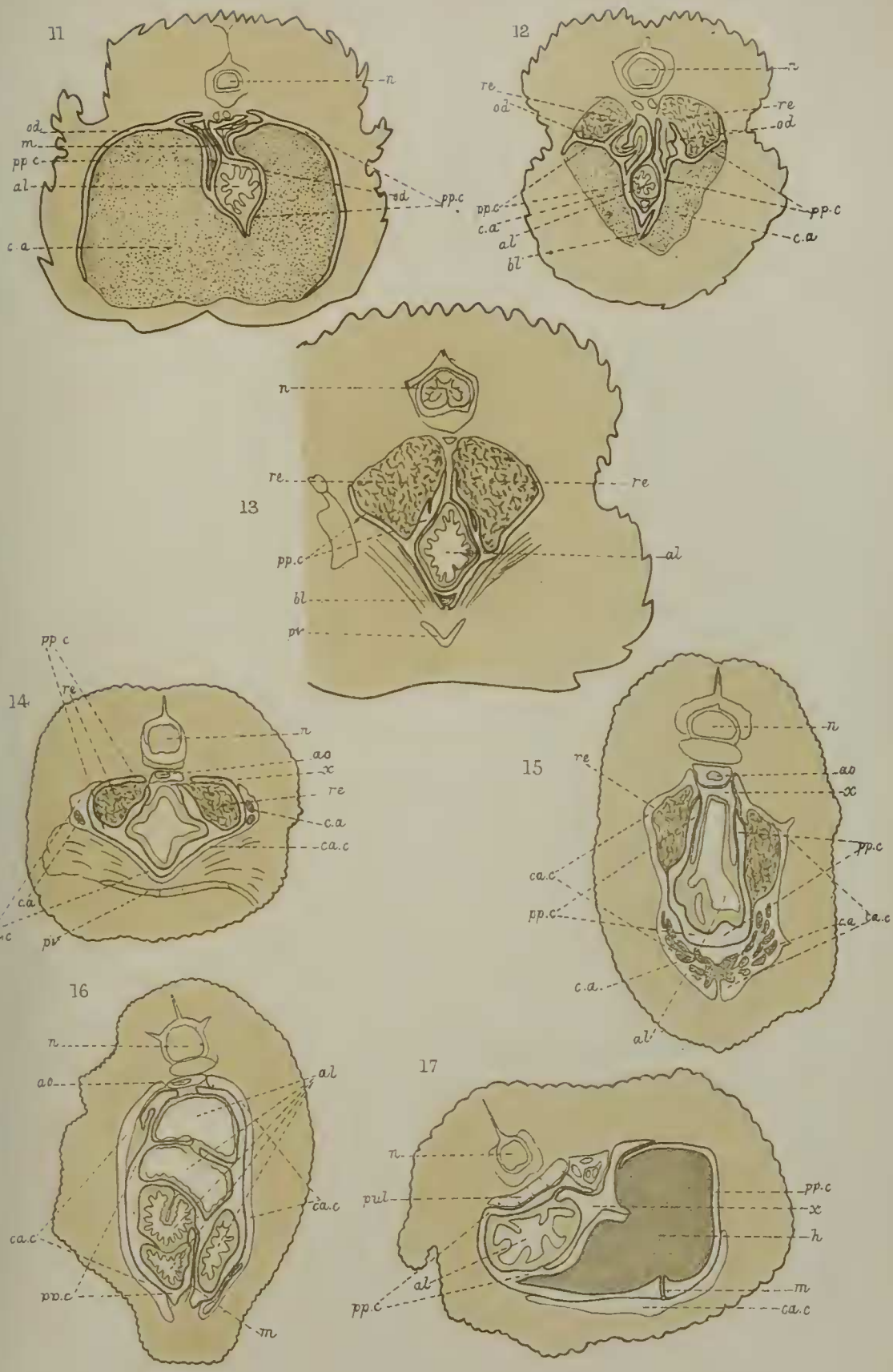
[1] Untersuchungen z. Morph. u. Syst. Vögel, Taf. xx. fig. 9.




G.W.Butler del. ad nat.
M.Parker lith

West, Newman imp.

Fat bodies in the Sauropsida.




G.W Butler del. ad nat.
M. Parker lith.

West, Newman imp

Fat bodies in the Sauropsida.

## I. Introductory.

The conditions under which the investigations of which this paper gives the results were commenced and carried on were stated in the introduction to my paper upon the Subdivision of the Body-cavity, read at the last meeting (see above, p. 452).

## II. On the Relations of the Fat-bodies of the Sauropsida, and on certain Points in the Anatomy of Monitors.

The fat-bodies referred to are those which, as is well known, occur in Lizards on the course of the "pelvic" veins, and of more or less of the anterior-abdominal vein. The vessels named, with their tributaries, take away the blood, which is brought to the fat-bodies by large branches from the anterior of the two pairs of arteries that supply the hind limbs, and which I take to be homologous with the femoral arteries of birds.

Corresponding fat-bodies are very conspicuous in the Snakes (*cf.* figs. 8, 9, & 10 *c.a*), where, as in the Snake-like Amphisbænidæ, they extend from the cloaca to the hinder margin of the liver (*cf.* figs. 4, 5, 6, 7). The figures of sections of Adder and embryo Grass-Snake show that, when the fat is well developed, the peritoneal cavity of Snakes may be much restricted by reason of the fact that the kidneys and fat-bodies lie outside it. The latter occur in the Crocodiles, but, as described below, the fat-bodies here referred to are in these animals more lateral in position than in Lizards; and in the case of the birds, the fat-laden "omentum," or transversely expanded ventral ligament of the stomach, is, I think, obviously comparable, so far as its fat is concerned, to the similar fat-laden ventral ligament in such forms as the Amphisbænidæ and Snakes, where the fat extends forwards as far as the liver.

The Chelonia are the only order of the Sauropsida in which I have not observed these structures well developed, but there appear to be traces of them in *Emys europæa*[1].

In many Lizards (*cf.* fig. 11) these fat-bodies, pushing the peritoneum before them, bulge into the body-cavity; and, lying on the course of the large vessels ventral to the (once respiratory allantoic) bladder (*cf.* figs. 7 & 12) and the alimentary canal, into the ventral ligament of which they in some forms (Amphisbænidæ, fig. 4) obviously extend, they may form paired masses quite as conspicuous in the posterior part of the abdominal cavity as are the liver-lobes in the anterior half[2].

[1] I have only examined in this connection some half-dozen specimens of *Emys* and *Testudo*, and those not large ones.

[2] These lie, of course, ventral to the alimentary canal and lungs. Passing over the important difference that no branching system of tubules extends from

The extent to which these fat-bodies project into the body-cavity varies, and that in a manner not merely dependent upon their size, but also, so to speak, upon the ease with which the peritoneum separates from the body-wall. In such a Lizard as *Tupinambis teguexin* I have seen the fat-bodies projecting forwards into the peritoneal cavity as two yellow lobes, as large as the liver-lobes; and this may be seen usually to a lesser degree in the common Green Lizard and in others. On the other hand, in a specimen of *Gerrhosaurus flavigularis* examined, these fat-bodies extend forwards into two spaces ventral to the peritoneum, without any free bulge into the body-cavity.

A series of transverse sections taken through an *Amphisbæna darwinii* (*cf.* figs. 4–7), or a dissection of the animal, show that while anteriorly to the umbilical region the fat-bodies bulge into the body-cavity, in the more posterior region the peritoneum is simply displaced inwards. Thus we have here the two conditions above referred to displayed in different parts of the same animal; and this is true, in a less striking manner, of other Lizards (*cf.* figs. 11 & 12), in which the hinder portions of the fat-bodies are obviously quite outside the peritoneal cavity.

The typical condition of these fat-bodies seems to be that of distinct lobed or festooned masses, suspended in distinct cavities [1] lined with smooth membrane, which are no part of the ordinary peritoneal cavity.

It seems to me that to the extension of these cavities, which surround the fat-bodies, outside the peritoneum, so as to carry it away from the body-walls, we must attribute the peculiar state of things in Monitors, described by Beddard: (1) Proc. Zool. Soc. 1888, pp. 98–107; (2) Anatomischer Anzeiger, 1888, pp. 204–206.

In the Monitors these two cavities communicate anteriorly, so as to form a single horseshoe-shaped cavity, with its free ends

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the alimentary canal into the substance of the fat-bodies, and regarding these and the liver simply as store-houses of combustible food-material, one is struck by the remarkable fore-and-aft symmetry displayed by the liver at one end of the trunk and the fat-bodies at the other, in their relations to the adjacent organs. And in this connection one is induced to comment upon the condition of the liver in *Siphonops annulatus* as described by Wiedersheim 'Die Anatomie der Gymnophionen,' p. 74, fig. 82):—"Die Leber stelt ein langes, bandartiges in zahlreiches Lappen zerfallendes Organ dar. Die einzelnen Lappen entstehen durch tiefe circulare Einschnitte, liegen schollenartig aufgereiht unt meistens in dichter gegenseitiger Berührung." The "Lappen" are in *Epicrium* "mehr gelblich gefärbt," while in *S. annulatus* they possess "eine mehr graugrüne Färbung."

Again, it may be worth while to note here the fate of the liver in *Petromyzon* (*cf.* Schneider, 'Beiträge z. verg. Anat. und Entwick. d. Wirbel.,' Berlin, 1879, pp. 93, 94); Rolleston ('Forms of Animal Life') says, "At the metamorphosis the tubular structure is lost; fat appears in the cells; the gall-bladder and bile-duct are absorbed."

It must be remembered, however, that (as described in this paper) the fat-bodies in some Reptiles project but slightly or not at all into the peritoneal cavity.

[1] It may be sometimes, however, hard to trace distinct spaces round these bodies.

pointing backwards, which in the hinder region extends up the sides as far as the kidneys.

I believe that the views to which I have been led largely agree with those of Mr. Beddard[1]. We agree that the condition in Monitors to which he has drawn attention is unlike that in other Lizards and well worthy of study. There are, however, certain of his conclusions and suggestions which, after a careful examination of Monitors[2] and other reptiles, I am unable to accept.

Beddard says (1, p. 100): "In Monitors . . . . . when the body-walls are cut open and reflected, the alimentary viscera are not exposed as they are in Iguana. A loose membrane covers the viscera; the membrane looks as if it were simply the lining peritoneum of the abdominal cavity which had got separated and detached from the abdominal parietes; this is, however, not the case; *an examination by the aid of the microscope showed clearly that a layer of peritoneum covers the abdominal musculature*, and is quite distinct from the horizontal membrane; in *Varanus griseus the peritoneal layer* was particularly distinct, for the reason that it contained numerous pigmented corpuscles. . . . *This horizontal membrane also separates the kidneys from the reproductive glands*; the latter lie internally to it; the kidneys are placed outside it."

The italics in the above quotation are mine, and serve to indicate the passages to which I would call attention.

It is certain that the space surrounding the fat-bodies and separated from the peritoneal cavity containing the intestines, by the "horizontal" membrane that wraps round these, is not due merely to some accidental or post-mortem separation of this membrane from the body-wall; and that the space in question, which I will term the *circumadiposal cavity* (*ca.c*, in figs. 14–17), is lined by a smooth membrane which covers the body-wall, and is reflected to form the exterior layer of the so-called "horizontal membrane."

I presume that, in saying that the microscope shows this lining membrane to be peritoneum, Beddard merely means that it forms a natural free surface, and is not a rough line of parting produced by a tear. More than this the microscope could not well prove; nor does the presence of pigment do so, since pigment, though common in the peritoneal lining of the body-cavity, is not confined to this layer. It may occur in the more external and muscular layers of the body-wall, as can be seen in transverse sections of Snakes.

Now, in no reptile examined have I observed any connection between the peritoneal cavity proper and the circumadiposal cavities; and since (as Beddard, judging by his paper (1, p. 100), would admit) the circumadiposal cavities of the Monitors are homologous with the inconspicuous spaces round the fat-bodies in other Lizards, which there is no good reason to regard as parts of the peritoneal cavity, I hold that until such a connection shall

[1] I would acknowledge the kind and practical interest that Mr. Beddard has taken in my work.

[2] I have examined two specimens of *Varanus indicus*, two of *V. nigro-punctatus*, and some ten small specimens of *V. niloticus*.

have been demonstrated, by a study of the development, everything points to the conclusion that the circumadiposal cavities are not homologous with any part of the peritoneal cavity proper of other types, but are altogether extra-peritoneal.

Again: I do not consider that the membrane "which surrounds the abdominal viscera has its exact counterpart in Crocodilia and Aves" (1, p. 106), except in so far as it is a part of the body-wall. I take it that the "omentum" of Birds is represented in Monitors by the ligament which passes between the stomach and the hinder part of the liver antero-dorsally, and the dorsal face of Beddard's horizontal membrane postero-ventrally. In Monitors, however, as in most other Lizards, it has not acquired that extension in a transverse direction which conduces to the formation of a *post-hepatic septum* in Birds, Crocodiles, and the Teiidæ (*cf.* my paper on the Subdivision of Body-cavity, above, p. 463).

As to the Crocodiles, Beddard says (1, p. 103) that the horizontal membrane "closely resembles a structure in the Crocodilia which has been described by Prof. Huxley as well as by others." Beddard describes this structure as follows (the italics are mine):—"This consists of a membrane, partly muscular, which is attached to the pubis and to the abdominal parietes behind, and in the median dorsal line to the backbone; it entirely envelops the coils of the intestines, so that they are not visible when the body-wall is cut through. Anteriorly this muscular expansion is attached to the fibrous compartments in which are lodged the two lobes of the liver; *the lungs are thus shut off from the abdominal cavity*; this membrane bears on the ventral surface the anterior abdominal veins: *there is evidently a close similarity, so far, between the Crocodile and the Lizard*; furthermore, in both animals the lateral regions of the membrane are connected with the lateral parietes by fibrous bands, and in both the fat-body lies outside of the membrane and outside of the abdominal cavity; the reproductive glands and the kidneys have a similar relation to the membrane in both types: in the Crocodile, as in the Lizard, *the reproductive glands and the kidneys are separated by the membrane*; the former lies within, the latter without, the abdominal cavity. The only differences are that in the Crocodile the membrane is largely covered by muscular tissue, and that instead of simply passing over the liver and stomach, it becomes connected with special sheaths enveloping these organs. In these points the Crocodile, as Prof. Huxley has pointed out, resembles birds. The above considerations point, in my opinion, to *an unmistakable resemblance between the Monitor Lizards and the higher Sauropsida.*"

I have not at present observed a well-marked circumadiposal space round the subperitoneal fat-bodies of Crocodiles. But if, as I take it, the membranes above referred to in Monitors and Crocodiles are but the inner layers of the body-wall, they are doubtless homologous to a certain extent. I would add, however, with reference to the statement that the membrane in Crocodiles is "largely covered with muscular tissue," that (in my opinion) the ventral fat-masses that

lie in distinct spaces beneath the skin, separated from the abdominal cavity by a stout muscular tract, are not the homologues of the *subperitoneal* fat-bodies of the Monitors, but of *subcutaneous* fat-deposits occurring in the Sauropsida in addition to the subperitoneal (*cf.* p. 609). The fat-bodies of the Crocodiles that correspond to those of Lizards are more lateral than is usual in the latter group.

Thus the membrane that is referred to by Beddard as being muscular in the Crocodile, according to the view here expressed represents, in the ventral region, a great part of the muscular body-wall.

In the quotations given above the position of the kidneys relatively to the so-called "horizontal membrane" has been referred to. A reference to figs. 14 and 15 shows that in *Monitor niloticus* the hinder portion of the kidney projects well into the peritoneal cavity which contains the intestines and reproductive glands, and that the part in front of this lies as it were *in* the membrane in question, or between its peritoneal and parietal layers; so that, though the anterior portions of the kidneys project outwards into the circumadiposal cavities, the membrane referred to does not exactly separate these from the reproductive glands.

But, even if the whole of the kidney were shut out of the general intestinal cavity, this would, I think, neither be a point of special similarity to the Crocodiles nor have much morphological significance. We find such a condition not only in the Crocodiles but in Chelonia (*Emys*, *Testudo*). In Snakes (*cf.* figs. 8, 9, 10), and in the Lizards themselves, the extent to which the kidneys project into the peritoneal cavity is variable, and the Amphisbænidæ are, so far as I know, unique in the freedom with which these organs hang into the peritoneal cavity.

In birds, again, the kidneys, as opposed to the reproductive glands, are extra-peritoneal in position (*cf.* figs. 46 and 47 of my paper "On the Subdivision of the Body-cavity," Plate XLIX. above, p. 452).

I think that the preceding points to the conclusion that the membrane which in Monitors is seen to cover the abdominal viscera when the body-wall is first cut into, must be regarded as the peritoneum, backed by the lining membrane of the space into which the fat-bodies project—that it, in fact, consists of the peritoneum together with another layer belonging to the body-wall.

With regard to the term "*horizontal*" membrane or septum it seems to me that it is used to comprise two things, which may with advantage be considered apart. There is, firstly, the membrane, referred to above, which divides the circumadiposal and peritoneal cavities. To this I would attach no particular morphological importance. It appears to me not to divide one part of the body-cavity proper from another, but to be, as Beddard (1, p. 100) seems fully to recognize, but a special development of a tract which occurs in other Lizards, correlated, as I would say, in Monitors with the greater extension of the circumadiposal spaces. In fact, in the separation of the membrane under discussion from the body-wall, the Monitors seem to be but following what is a line of weakness for Reptiles

generally. Thus, in the Snakes, Chelonia, Lizards, and Crocodiles, there is a more or less marked tendency to the separation of the inner peritoneal or visceral layer of the body-wall from the rest, the kidneys and fat-bodies being thus left more or less completely outside the peritoneal cavity.

On the other hand, Beddard's phrase (1, p. 105),—"the horizontal membrane in *Varanus*, which shuts off both lungs from the abdominal cavity,"—together with the reference which follows to the "membranous diaphragm" described by Martin (P. Z. S. 1831, p. 138), indicates that it is used to include tissue which shuts off the lungs from the peritoneal cavity. Here we have a fact of considerable interest; and neither the dissections nor the transverse microscopic sections that I have made have rendered it plain whether, as in birds, a pleural cavity originally exists, to be subsequently obliterated by adhesions, or whether, as I believe to be the case in *Testudo*, the lungs are not surrounded by any part of the body-cavity. Whichever be the case, the separation of the lungs by a "membranous diaphragm" from the peritoneal cavity which contains the liver and intestines is a feature that, so far as I know, is not found in any other Lizard. But, on the other hand, the lungs and liver are not thus separated in the Crocodiles either (*cf.* my paper "On the Subdivision of the Body-cavity &c.," § v. this vol.).

The preceding pages will show that in my opinion the Monitors bear no special resemblance to the Crocodiles, so far as the relations of the fat-bodies and the spaces and membranes about them are concerned. The shutting off of the lungs from the liver, while suggesting the condition in the birds, distinguishes them from the Crocodiles, and, in the absence of developmental data, it may be perhaps just as well explained by a reference to *Testudo*[1].

Again, seeing that some striking differences exist as to the subdivision of the body-cavity in the other Lizards (*cf.* the case of the Teiidæ above, Plate XLVIII. and text, p. 466), it appears to me doubtful whether, in our ignorance of the developmental history, the shutting off of the lungs from the peritoneal cavity in the Varanidæ has much or little significance for the systematist.

### III. Subperitoneal Fat of Mammals.

To turn to animals outside the Sauropsida, we find among mammals deposits of fat on either side of the bladder (*e. g.* Kitten, Guinea-pig, Hedgehog, young Kangaroo). It is impossible in some cases to definitely mark off the fat in this position from that which passes forwards on the dorsal side to the kidneys; and both are supplied by branches from the femoral artery (Guinea-pig). If this vessel is the homologue of the femoral artery of Sauropsida, which supplies the fat-bodies (Lizards)—seeing that in Lizards, Crocodiles,

[1] *Emys*, in which the lungs only partly project into the body-cavity, would seem to stand as a link between *Testudo* and the majority of animals that have the lungs fully projecting into the cœlom, and to show that even such a striking feature as the exclusion of the lungs from the body-cavity may be of comparatively little systematic importance.

and Birds, owing to the backward extension of the kidneys, the fat-bodies in question do practically adjoin them—it becomes by no means improbable that the fat beneath the dorsal peritoneum posterior to the kidneys in mammals is the homologue of, or rather belongs to, the same series of deposits as the fat-bodies of the Sauropsida.

But the habit, so to speak, of these deposits in the two groups is considerably different. The Sauropsida with their backwardly situated kidneys, renal-portal system, and anterior abdominal veins, have these fat-masses either confined to the region just in front of the pelvic girdle, or extending right along on the ventral side as far as the stomach and liver; whilst in Mammals, where the vascular system is different, they are mainly dorsal in position.

## IV. Some Remarks on the Function of the Subperitoneal Fat-bodies of the Sauropsida.

If, as above suggested, these fat-deposits in the Sauropsida correspond to those, so common in Mammalia, behind the kidneys, there would appear to be no more reason to seek a special function for them in one group than in the other, as some observers have done for the Reptiles.

These bodies, like the liver, can be regarded as stores of food-matter on the course of large blood-vessels, and of course they will be drawn upon whenever need arises—whether in the "winter sleep," as appears to have been usually assumed, or in the production of large masses of yolk for the eggs, or at any other time when food may be unattainable.

It should be noted that in both Amphisbænidæ and snakes (*A. darwinii* and *Tropidonotus natrix*), when still within the eggs (*cf.* figs. 4–7, 8, 9, 10), the fat-bodies are as well, or better, developed (proportionally) than at any subsequent period of life. This, together with the fact that there seems no marked difference in their size in the two sexes, would seem to show that their function is a general one and not specially related to reproduction, as has been suggested.

## V. On Certain Subcutaneous Fat-deposits.

In Lizards we have fat ventral to the pelvic girdle (between it and the skin) and extending along the under part of the thigh and surrounding the "femoral glands" (when present). This seems to have no continuity with the *subperitoneal* fat-bodies above described. In the Crocodiles both the *subcutaneous* and the *subperitoneal* fat seem to be fairly well developed, the former being separated from the abdominal cavity by a muscular tract, which I think is that referred to by Beddard (1, p. 103, see above pp. 606 & 607) and compared to what he terms the "horizontal membrane" in Monitors. It appears to me, however, that only the lateral fat-masses of Crocodiles correspond to the ventral subperitoneal "fat-bodies" of the Lizards, and that the ventral deposits in Crocodiles belong to the subcutaneous series. Consequently the muscularity of the layer of tissue